

BREEDING ECOLOGY OF SEASIDE SPARROWS IN A MASSACHUSETTS SALT MARSH

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ABSTRACT.—Seaside Sparrows (*Ammodramus maritimus*) were observed during the breeding seasons of 1985 and 1986 in a 151-ha salt marsh/tidal pond complex in Massachusetts near the northern range limit for the species. The study marsh is ditched and is dominated by salt meadow grasses (*Spartina patens*, *Distichlis spicata*, *Juncus gerardi*) and the high marsh form of *Spartina alterniflora*. Territories generally were isolated from one another; however, six relatively small territories were clustered into an area of the marsh rich in suitable nesting and foraging sites. The mean size of 17 territories measured in 1985 was 3953 m². Territories contained more tidal creek, medium-height *S. alterniflora*, and persistent-growth *S. alterniflora* than was expected, based on the results of line-intercept vegetation sampling done within randomly placed plots. Eighty-two percent of 60 nests found were placed in irregularly flooded *S. alterniflora* habitats, and 54% were placed in medium height *S. alterniflora* stands that occurred as approximately 2-m wide strips adjacent to creeks and ditches. One-half of all nests found were lost to flooding by spring tides which simultaneously destroyed most active nests on the marsh in May of each year. The rapid renesting response of most sparrow pairs following flooding events resulted in a synchronization of nesting activities with the tidal cycle. Synchronized nests had an enhanced probability of survival since the nesting cycle could be completed prior to the next spring tidal inundation. Overall, nest success was highest for nests initiated after 20 June, due to the increased probability of renesting attempts being synchronized to the tidal cycle, and because of the seasonal growth of marsh grasses which provided a more elevated nest substrate. Received 6 June 1989, accepted 1 Nov. 1989.

Although substantial work has been done on populations of the northern race of the Seaside Sparrow (*Ammodramus m. maritimus*) occupying Long Island, New York, marshes (Post 1974; Post and Greenlaw 1975, 1982; Greenlaw 1983; Post et al. 1983; Greenlaw and Post 1985), few investigations have been conducted in southern New England, close to the northern range limit for the species. Here populations are uncommon and relatively small, and are susceptible to local extirpation. Reinert et al. (1981), Stoll and Golet (1983), and DeRagon (1988) have conducted the only recent New England studies. They determined patterns of Seaside Sparrow habitat use in Rhode Island salt marshes.

In this paper, we report on aspects of habitat selection and breeding biology of a Massachusetts Seaside Sparrow population (ca 24 pairs) occurring only 137 km south of the northern range limit of the species. Our

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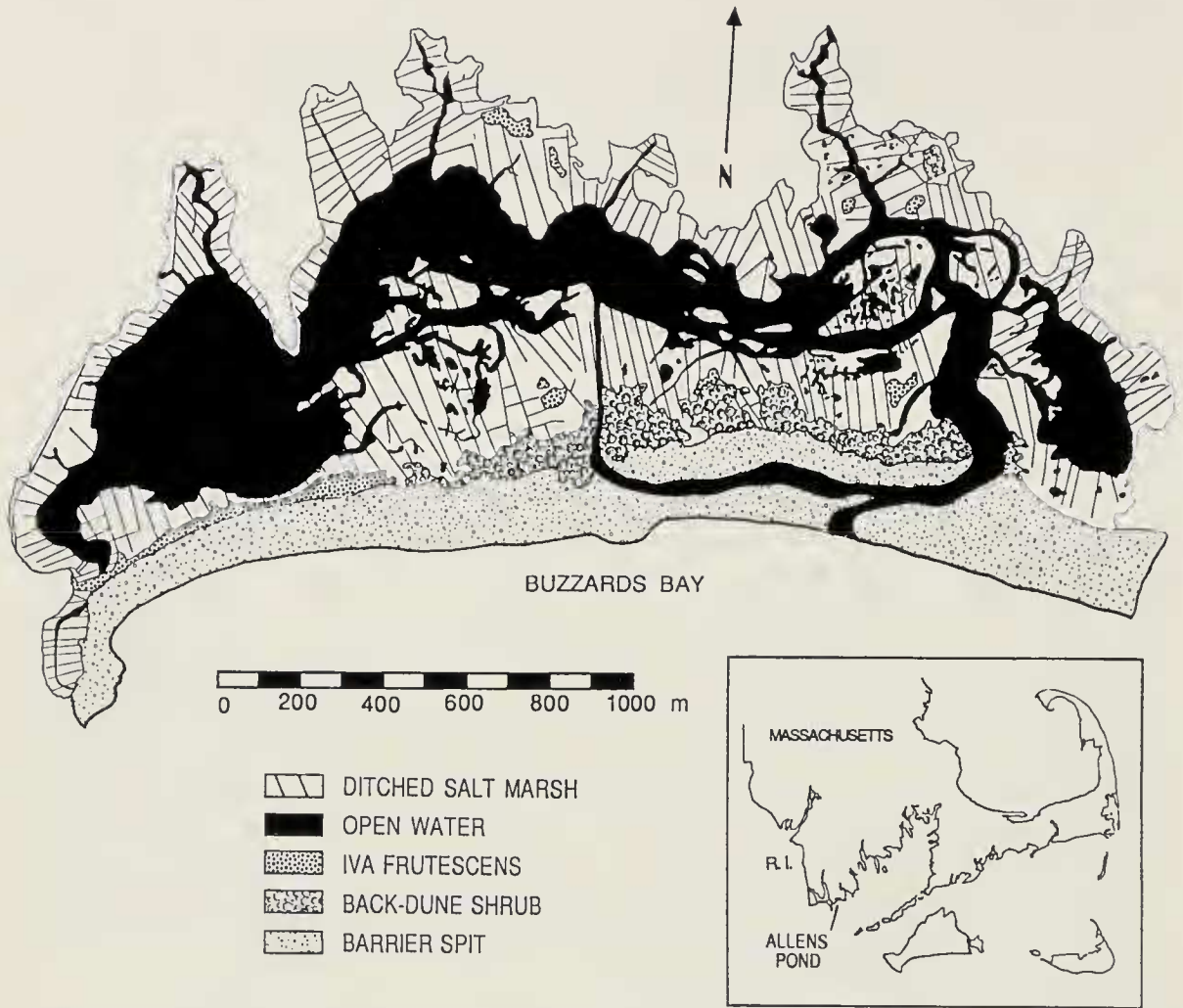


FIG. 1. Allen's Pond, South Dartmouth, Massachusetts, illustrating the intensity of mosquito ditching in the salt marsh. Back-dune shrub is dominated by bayberry (*Myrica pennsylvanica*) and poison ivy (*Rhus radicans*).

study site differs substantially from other North Atlantic marshes inhabited by this race in the distribution and composition of marsh vegetation, frequency of catastrophic flooding events, and resultant patterns of habitat selection and mortality. We address such differences as they relate to patterns of Seaside Sparrow habitat use and factors affecting nest success.

STUDY AREA

Allen's Pond is a 67-ha tidal pond located in South Dartmouth, Bristol County, Massachusetts ($41^{\circ}31'N$; $71^{\circ}00'W$). The pond is connected to Buzzards Bay by a tidal inlet (Fig. 1), and is bordered on all sides by salt marsh totaling 91 ha. A 35-ha barrier beach/dune system lies adjacent to the salt marsh to the south, with maritime oak forest, agricultural fields, and shrub communities bordering to the east, north, and west.

Prior to mid-century, the salt marsh was ditched extensively for mosquito control (Fig. 1). Linear ditches, 0.5–1.0 m wide, transect the salt marsh at 30 to 40-m intervals throughout its entire expanse, extending from Allen's Pond to the upland edge of the marsh. Although

most ditches remain open, they have not been maintained and many have become filled to varying degrees, lessening the flow of tidal water through them. To a lesser extent, naturally formed tidal creeks, and irregularly flooded pools occur throughout the marsh.

The interior of the marsh is dominated by irregularly flooded high marsh vegetation, chiefly *Spartina patens*, *Distichlis spicata*, and *Juncus gerardi* (hereafter "salt meadow"), and the short form (<40 cm) of *S. alterniflora* (hereafter "short SA"; Niering and Warren 1980, Greenlaw 1983). Sparse stands of short SA grow on the most poorly drained areas of the high marsh adjacent to, or mixed with, salt meadow graminoids. Although the tall (>100 cm) low marsh (regularly flooded) form of *S. alterniflora* is nearly absent, an irregularly flooded, intermediate form (40–100 cm tall) (hereafter "medium SA"; Greenlaw 1983), grows in a zone between the elevations of the low marsh and salt meadow. Medium SA most commonly grows in dense 1- to 2-m wide stands along creeks, ponds, and mosquito ditches (hereafter "water-side SA"). It often persists as clumped, erect, brown stems throughout the winter and subsequent growing season. Stands of medium SA sometimes extend 10–20 m into the marsh interior and, in some areas fill the entire inter-ditch span. Where short SA grows adjacent to water, it also forms dense, persistent stands, similar to medium SA in all aspects but height.

Small islands (4–100 m²) created by the deposition of spoil are scattered throughout the marsh and are dominated by *Iva frutescens* and *J. gerardi*. Those plants are also dominant where the tidal marsh grades into the upland.

METHODS

Observations of Seaside Sparrows were made between 05:00 and 10:00 or 18:00 and 20:30 EST on 46 days from 1 May–25 August in 1985, and on 61 days from 30 April–22 August in 1986. Adults were trapped with mist nets and banded with a U.S. Fish and Wildlife Service aluminum band on one leg and a unique combination of two colored celluloid bands on the opposite leg. Nestlings were banded five to six days after hatching with an aluminum band placed on the right leg in 1985 and on the left in 1986. We banded 13 adult (seven male, six female) and 35 nestling Seaside Sparrows in 1985, and 18 adults (12 male, six female) and 58 nestlings in 1986. Territories were mapped using the flush method (Wiens 1969) and by observing birds remotely with the aid of a spotting scope. Songposts were plotted on 1:985 scale cover maps of the area. Territories were delineated by connecting the outermost songpost plots on the cover maps (Odum and Kuenzler 1955), and territory size was subsequently determined with a compensating polar planimeter.

In 1985, the percent cover of each habitat occurring within 17 Seaside Sparrow territories and 17 randomly located circular plots was estimated by the line-intercept method (Canfield 1941, Reinert and Golet 1979). Each random plot was 3953 m², the mean area of the 17 Seaside Sparrow territories. Sampling was done along two perpendicular transect lines which crossed at the center of the territory/plot. The habitat composition was not estimated within seven territories for which we had inadequate data on territory boundaries. We tested for significant differences ($P \leq 0.05$) in habitat composition between territories and random plots, using unpaired *t*-tests for each habitat type. Plant height measurements were made within all *S. alterniflora* segments. Measurements were made at the center of segments <5 m in length, and at four evenly spaced points within segments >5 m. In addition, the presence or absence of persistent stems was noted for each *S. alterniflora* patch intercepted.

For each nest located, the height of the nest (substrate to rim), height of surrounding vegetation, and distance to nearest open water were measured. Nests were visited approximately every four days during nest building and egg-laying and every other day during the incubation and nestling stages. We used the methods of Mayfield (1975) and Ricklefs and Bloom (1977), respectively, to calculate nest success and breeding productivity.

RESULTS

Population size and philopatry.—Twenty-four mated males occupied the study area during the 1985 breeding season. In 1986, 29 males were located, 24 of which were mated. In each year, males arrived during the first week of May, and females were first observed during the third week of May. Four (30.8%) of 13 adult Seaside Sparrows banded on the study area in 1985 returned in 1986. The territories of three (two male, one female) overlapped those which they occupied in 1985, and the territory of the fourth bird (male) was approximately 100 m from that defended in 1985. None of the 35 nestlings banded in 1985 was seen in the study area in 1986.

Territories.—The mean size of 17 territories for which adequate boundaries were determined in 1985 was 3953 m² (range = 1290–10,423 m²). During both years, a central portion of the marsh, where tidal creeks, pools, and mosquito ditches are relatively abundant, contained an aggregation of six territories whose boundaries were adjacent or overlapping. The remaining territories were widely distributed throughout the marsh in each year. The aggregated territories were significantly smaller ($t = 2.23$; $P < 0.05$) than isolated territories ($\bar{x} = 1814$ m² vs 4730 m², range = 1290–2581 m² vs 1411–10,423 m², $N = 6$ vs 11, respectively).

Male Seaside Sparrows which occupied territories within the interior of the marsh perched and sang nearly exclusively from patches of clumped, persistent vegetation, especially from stands of water-side SA. Stems of *I. frutescens* and *Phragmites australis* were the most frequently used song-posts of males which occupied territories near the upland edge of the marsh.

Our observations indicate that Seaside Sparrows foraged exclusively within territory boundaries, and although we did not quantify the use of habitats for foraging, our observations revealed that the banks and exposed bottoms of mosquito ditches and tidal creeks were the principal foraging areas. Birds also foraged within sparse stands of short SA when it was available within their territories.

Fig. 2 compares the habitat composition of Seaside Sparrow territories with that of the random plots. There was a significant difference for tidal creek only, which was more abundant in territories (\bar{x} percent cover = 18.0 vs 2.5, $t = 3.6$, $P < 0.001$). The six aggregated territories measured in 1985 contained more overall SA area (60 vs 40%), and water-side SA area (28 vs 17%), and less salt meadow (22 vs 38%), than the non-grouped territories. However, none of those differences was significant.

Nest-site selection.—Seaside Sparrow nest sites at Allen's Pond were categorized into three early-season (nests started on or before 20 June)

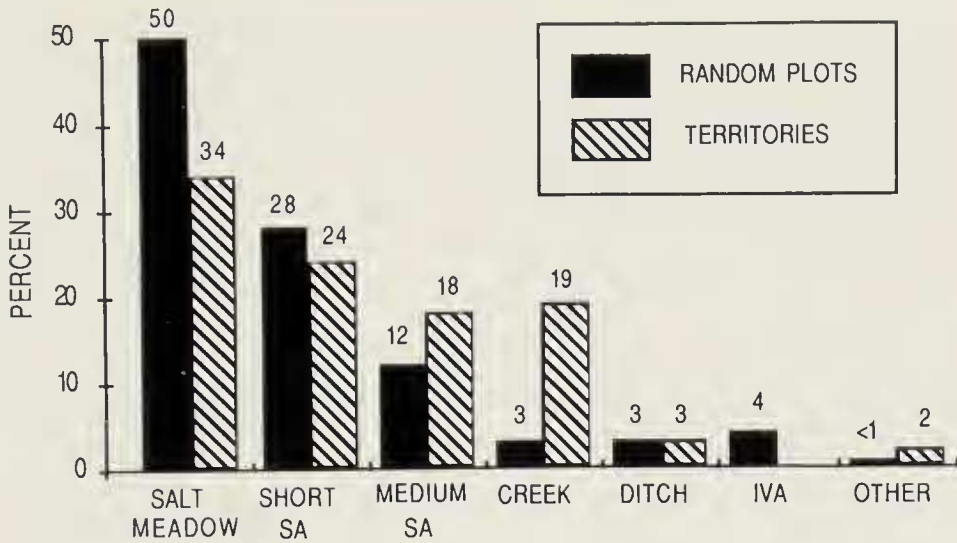


FIG. 2. Mean percent cover of habitats in 17 Seaside Sparrow territories and 17 random plots measured in 1985.

and two late-season (nests started after 20 June) types (Table 1). In both years, the height of new herbaceous vegetation exceeded that of persistent stems on or before 20 June, after which new growth became the primary substrate within which nests were placed.

Eighty-seven percent of all early-season nests were placed in clumped and erect persistent vegetation. Medium height persistent *S. alterniflora* was the tallest herbaceous cover on the marsh at this time (Table 1), and

TABLE 1
NEST-SITE CHARACTERISTICS AND NEST SUCCESS OF EARLY- AND LATE-SEASON^a SEASIDE SPARROW NESTS IN DIFFERENT HABITATS^b IN 1985 AND 1986

	N	Mean (\pm SD) height of nest (cm)	Mean (\pm SE) height of vegetation at nest (cm)	Number of nests within 2 m of water (%)	Number of successful nests (%) ^c
Early-season nests					
Persistent SA	30	18.7 \pm 4.54	42.1 \pm 8.39	13 (43)	7 (23)
Persistent SM	4	15.5 \pm 2.88	31.5 \pm 5.44	0	1 (25)
New growth SM	5	11.4 \pm 1.97	32.9 \pm 8.74	3 (60)	1 (20)
Late-season nests					
New growth SA	19	21.9 \pm 5.56	52.7 \pm 14.82	14 (74)	13 (68)
New growth SM	2	12.0	38.8	1 (50)	1 (50)

^a Early-season nests were initiated on or before 20 June; late-season nests were initiated after that date.

^b SA = *Spartina alterniflora*, SM = salt meadow.

^c Successful nest = at least one young fledged.

30 (77%) of 39 early-season nests were placed in this habitat. Three early-season nests (8%) were placed in stands of persistent *D. spicata*, and one nest was placed in a mix of *S. patens* and *S. alterniflora*. Four of the remaining five (10% of total) early nests were placed within new growth *J. gerardi* which attained its maximum height by mid-June. One nest was placed in a stand of new growth *S. patens* on an elevated spoil bank.

Nineteen (90%) of 21 late-season nests were placed in new growth *S. alterniflora* habitats. The *S. alterniflora* stems surrounding those nests were significantly taller than the persistent stems that surrounded early-season *S. alterniflora* nests ($\bar{x} = 52.7$ vs 42.1 cm, respectively; $t = 2.83$, $P < 0.001$), and late season *S. alterniflora* nests were significantly higher than early-season nests ($\bar{x} = 21.9$ vs 18.7 cm, respectively; $t = 2.13$, $P < 0.04$) (Table 1). The two remaining late-season nests were placed in new growth *J. gerardi*.

Thirty-one (54%) nests were placed in stands of water-side SA. Those stands were significantly taller than stands of *S. alterniflora* occurring more than 2 m from water bodies ($\bar{x} = 51$ vs 31 cm, $t = 10.45$, $P < 0.001$), and the nests placed within them were significantly higher than other *S. alterniflora* nests ($\bar{x} = 20.3$ vs 16.8 cm, $t = 2.70$, $P < 0.009$). Also, stems of persistent *S. alterniflora* occurred more frequently in water-side stands than in other stands of *S. alterniflora* (50 vs 20%). Twenty (65%) of the water-side nests were placed adjacent to mosquito ditches and 11 (35%) adjacent to tidal creeks.

Nesting biology.—The first known egg dates for 1985 and 1986 were 25 May and 26 May, respectively. The last known egg-laying date in 1985 was 7 July, and in 1986 was 30 July. The mean clutch size was 4.0 (N = 30) in 1985 and 3.9 (N = 25) in 1986. Clutch size in 1985 ranged from three (four nests) to five eggs (two nests) and in 1986 from two (one nest) to five eggs (one nest). The single two-egg clutch (1986) was initiated by a pair that was still tending to a single young which had left the previous nest only six days earlier. All five-egg clutches were laid during first nest attempts.

Observations of nine nests found during egg laying indicate that incubation began with the laying of the last egg. The mean incubation period (number of days from last egg laid to last egg hatched) for seven nests with complete data was 12.4 ± 0.97 days (range = 11–14 days).

The mean nestling period (number days from first egg hatched to first young fledged) during both years was 9.6 ± 0.51 days (N = 22; range = 9–11 days).

We observed the total number of days elapsed from the initiation of nest construction to the fledging of the last young for 12 nests found

during both years. Two nestings were completed in 27 days, eight in 28 days, one in 30 days, and one in 36 days ($\bar{x} = 28.7$ days).

Nest failure and renesting.—Due to the destruction of nests by spring and/or storm-driven tidal flooding, nesting attempts for many pairs were interrupted up to three times during both years. Of 60 nesting attempts observed during both years, 37 (62%) were unsuccessful. Of the nests lost, 81% were destroyed by spring tide flooding events (three events in 1985 and two in 1986), 5% were destroyed by a storm tide, and 3% were lost during two continuous days of rain and cold temperatures. Nest predation was not witnessed, but American Crows (*Corvus brachyrhynchos*) and Common Grackles (*Quiscalus quiscula*) were believed to be responsible for 11% of the nest losses.

Seaside Sparrows repeatedly renested following nest failure, and they also renested after fledging young from a previous nest. For both years combined, we documented that 16 pairs nested at least twice, and seven pairs nested at least three times. However, based on all evidence (e.g., empty nests found, behavior of adults), we suspected that 25 pairs nested at least twice and that 14 pairs nested three times.

We obtained complete chronological data for four renests following nest destruction. The mean inter-nest period (the number of days from nest failure to the day the first egg of the new clutch is laid) for those nests was 6.25 ± 1.7 days (range = 4–8 days). By back-dating from a known hatch date (assuming a 12-day incubation period and laying rate of one egg per day), we estimated a mean inter-nest period of 5.7 ± 1.0 days for an additional 11 nests initiated following nest failure (five days, $N = 6$; six days, $N = 3$; seven days, $N = 1$; eight days, $N = 1$).

In 1985 one female laid the third egg of a new clutch on the same day the single young from the previous nest fledged. We estimated inter-nest periods of eight and nine days from two nests in which at least one young fledged successfully from the previous nest attempt.

Nest success.—We defined a successful nest as that from which at least one nestling fledged. In 1985, 33 nest attempts produced 13 (39%) successful nests and 37 fledglings. In 1986, 27 nest attempts produced 10 (37%) successful nests and 27 fledglings.

Measures of the success rate (Mayfield 1975) for early- and late-season nests are presented in Table 2. In both years, most young fledged in July from second or third nest attempts of their parents (Fig. 3). Because most pairs renested immediately following nest loss, the simultaneous loss of many early-season nests due to tidal inundation acted to synchronize the subsequent nesting attempts of the unsuccessful pairs (Fig. 3). The young of those renesting pairs fledged nearly simultaneously, just prior to, or at

TABLE 2
NEST SUCCESS OF EARLY- AND LATE-SEASON^a SEASIDE SPARROW NESTS

	1985			1986		
	Early-season nests	Late-season nests	Overall	Early-season nests	Late-season nests	Overall
Number of nests	20	10	30	14	11	25
Mean clutch size	4.1	3.8	4.0	3.8	4.0	3.9
Clutch survival ^b	0.347	1.0	0.482	0.888	1.0	0.945
Brood survival ^b	0.408	0.777	0.579	0.480	0.589	0.536
Probability egg will produce fledgling	0.108	0.637	0.221	0.326	0.548	0.426

^a Early season nests were initiated on or before 20 June; late season nests were initiated after that date.

^b After Mayfield (1975); based on 12 day incubation period, and/or 10 day nestling period.

the time of, the next spring tide (Fig. 3). Nest cycles extended as little as one day due to large clutches, or protracted incubation or nestling periods, were subject to destruction if their nests were not high enough to avoid the tides. We witnessed nestling sparrows literally climb from their nests as they avoided encroaching tides, and in one nest we observed a nestling drown two siblings while elevating its own body above the flood-water.

Late-season nests were also higher than early nests as a result of the seasonal growth of *S. alterniflora* which supported most of them (Table 2). For the two years combined, 68% of all young fledged from late-season nests that were placed in the taller new-growth *S. alterniflora*. Overall, 83% of all young fledged from *S. alterniflora* nests.

Successful early-season nest attempts of the two years resulted when either: (1) nest elevation was particularly high and flood waters were avoided, or (2) nests were flooded during the egg-laying period when eggs did not float from them.

Due to the high success rate of late-season nests in 1985, overall productivity (number of young fledged per female; Ricklefs and Bloom 1977) was greater in that year than in 1986 (4.47 vs 3.46 young/female, respectively). However, the probability of an egg producing a fledgling was greater in 1986 due to the greater proportion of eggs that survived to the nestling stage (Table 2). Ninety percent (87 of 97) of all eggs hatched in 1986, whereas only 56% (70 of 124) of all eggs hatched in 1985.

DISCUSSION

Nest success. — Factors relating to nest success in the Northern Seaside Sparrow have been documented for only two geographic areas: the south shore of Long Island, New York (Post 1974, Post and Greenlaw 1982,

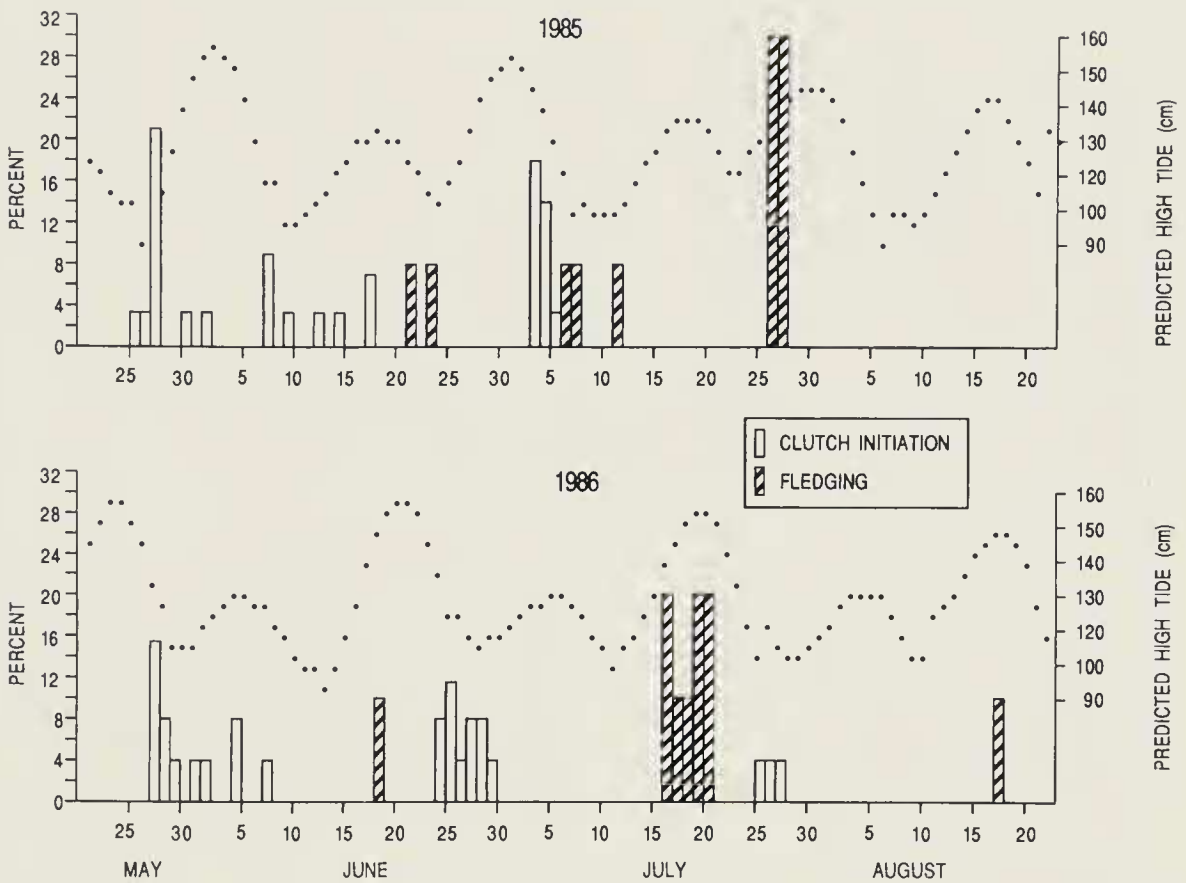


FIG. 3. Seasonal distribution of clutch initiation and fledging events in relation to the monthly tidal cycle. Bars represent the percent of total events, plots represent the predicted elevation of daily high tides relative to mean sea level for Newport, Rhode Island (White 1985, 1986).

Post et al. 1983), and our Allen's Pond study site in southeastern Massachusetts. In both areas, nest mortality was high, and nest failure related principally to catastrophic flooding events which destroyed, simultaneously, most active nests on the marsh. Predation rates were low at both sites. Flooding events in New York were associated with wind-driven tides and rain associated with storms; spring (moon) high tides under normal circumstances did not flood nests. At Allen's Pond, however, two spring tide flooding events in 1985 and 1986 reached sufficient elevation to destroy most nests. Thus, potentially catastrophic events occurred, predictably, every 28 days with the onset of spring tide cycles.

Because of this phenomenon, the renesting response of sparrows following nest loss, and the height of the nest, were the principal factors relating to nest success in this population. The probability of fledging young was greatest for late-season nests when marsh vegetation was tallest, and when nesting activities were more likely to be synchronized to the tidal cycle due to previous spring-tide related nest destruction.

TABLE 3
HABITAT AND TERRITORY CHARACTERISTICS OF SEASIDE SPARROW POPULATIONS IN THE NORTHEAST

	Ditched marches			Unditched marshes	
	New Jersey ^a	New York ^b	Rhode Island ^c	Massachusetts ^d	New York ^b Rhode Island ^c
Mean size of territories (m ²)	—	4669	9010	4730 ^e 1814 ^f	484 4545
Territory type(s)	(1) Separate nesting and feeding (2) All purpose	All purpose ^g	All purpose ^g	All purpose ^g	Defended nesting with communal feeding area (1) Separate nesting and feeding (2) All purpose
Distribution pattern(s) of territories	Widely spaced	Widely spaced	Widely spaced	(1) Widely spaced (2) Clustered	Clustered Clustered
Dominant marsh vegetation	Salt meadow	Salt meadow	Salt meadow	Salt meadow	Medium SA Medium SA
Nest site type(s) (n)	Juncus/Iva (8)	Salt meadow	(1) Juncus/Iva (1) (2) Medium SA (1)	(1) Medium SA (49) (2) Salt meadow (11)	Medium SA (1) Medium SA (26) Salt meadow (6)

^a Woolfenden (1956).

^b Post (1974).

^c DeRagon (1988).

^d This study.

^e Mean size of 11, non-clustered territories (see Results).

^f Mean size of 6 clustered territories (see Results).

^g Type A territories of Nice (1937).

The length of breeding season, probability of an egg producing a fledgling, and overall productivity were similar between our Allen's Pond study site and the New York populations (Post and Greenlaw 1982). However, the total number of young recruited per unit area of marsh should be much greater in New York, since nearly all suitable habitat is occupied (Greenlaw 1983). Expansive areas containing apparently suitable habitat (as assessed by early-season availability of cover) were left unoccupied by Seaside Sparrows at Allen's Pond.

Habitat use.—For northern-race populations of the Seaside Sparrow, nest site requirements are commonly met in one of two types of marsh vegetation. In the first, nests are placed within erect clumps of persistent or new-growth medium SA (Post 1974, Greenlaw 1983, DeRagon 1988, the present study). Medium SA nest sites are most commonly used on poorly drained, unditched marshes where *S. alterniflora* habitats are abundant. Territories on these marshes typically are clustered and relatively small (Table 3). In the second type, nests are placed in the cover of the salt meadow graminoids, *S. patens*, *D. spicata*, or, most commonly, *J. gerardi*, which occur on relatively high areas of the marsh. These nest sites typically are used on salt-meadow dominant marshes that have been ditched for mosquito control. *S. alterniflora* habitats are not abundant, and patches of *J. gerardi*/*I. frutescens* prevail on spoil islands or spoil ridges which occur adjacent to the ditches (Woolfenden 1956, Post 1974, Greenlaw 1983, DeRagon 1988, the present study). Territories on these marshes are generally large and widely spaced (Table 3).

Among marshes where investigations of the northern race of the Seaside Sparrow have been conducted, Allen's Pond is unique in that each type of nesting habitat that has been documented for the species (see above) is widely distributed throughout the marsh. Foraging habitats, including ditches, creeks, and short SA, are also widely distributed. Although the marsh is dominated by salt meadow habitats, the widespread distribution of ditches and creeks (Fig. 1), each bordered by medium SA habitat, serves to break up the marsh physiognomy and create an interspersion of habitats which provides Seaside Sparrows a variety of habitat-use choices throughout the marsh. This configuration of habitats at Allen's Pond provided a natural experiment for determining nest-site preference. Although medium SA made up only 12% of the cover on the marsh, 82% of the nests were placed in that habitat. Only 18% of the nests were placed in salt meadow habitats which covered one-half of the marsh. This clearly indicates a preference for *S. alterniflora* nest sites, regardless of the fact that it was present in the form of narrow strips adjacent to ditches and creeks. Thus, although marshes ditched for mosquito control have been associated with salt-meadow nest sites in widely spaced territories and relatively

low population densities, it is clear that the composition and configuration of marsh habitats, regardless of prior ditching history, determines the manner in which Seaside Sparrows will utilize marsh resources.

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